Revisiting the von Bertalanffy Seasonal Cessational Growth Function of Pauly et al. (1992)

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April 29, 2016

Introduction

The mean length-at-age for many animals (e.g., CITATIONS) is often modeled with the von Bertalanffy growth function (VBGF; von Bertalanffy (1938)). The parameterization of the VBGF attributable to Beverton and Holt (1957) is most common and may be expressed as

$$L_t = L_\infty(1 - e^{-q}) \qquad (1)$$

with

$$q = K(t - t_0) \qquad (2)$$

where $L(t)$ is the expected or average length at time (or age) t, L_∞ is the asymptotic mean length, K is a measure of the exponential rate of approach to the asymptote (Schnute and Fournier 1980), and t_0 is the theoretical time or age (generally negative) at which the mean length would be zero.

Many animals exhibit seasonal oscillations in growth as a response to seasonal changes in environmental factors such as temperature, light, and food supply (CITATIONS). Equation 2 of the traditional VBGF has been modified, usually with a sine function, to model these seasonal oscillations in growth. The most popular of these modifications is from Hoenig and Choudaray Hanumara (1982) and Somers (1988) (and carefully reiterated in Garcia-Berthou et al. (2012)), and uses

$$\begin{aligned} q =& K(t - t_0) \\ &+ \frac{CK}{2\pi} sin(2\pi(t - t_s)) - \frac{CK}{2\pi} sin(2\pi(t_0 - t_s)) \end{aligned} \qquad (3)$$

where C modulates the amplitude of the growth oscillations and corresponds to the proportional decrease in growth at the depth of the oscillation (i.e., "winter"), and t_s is the time between time 0 and the start of the convex portion of the first sinusoidal growth oscillation (i.e., the inflection point). If C=0, then there is no seasonal oscillation and Equation 3 reduces to Equation 2 and the typical VBGF (Figure 1). If C=1, then growth completely stops once a year at the "winter-point" (WP), whereas values of 0<C<1 result in reduced, but not stopped, growth during the winter (Figure 1).

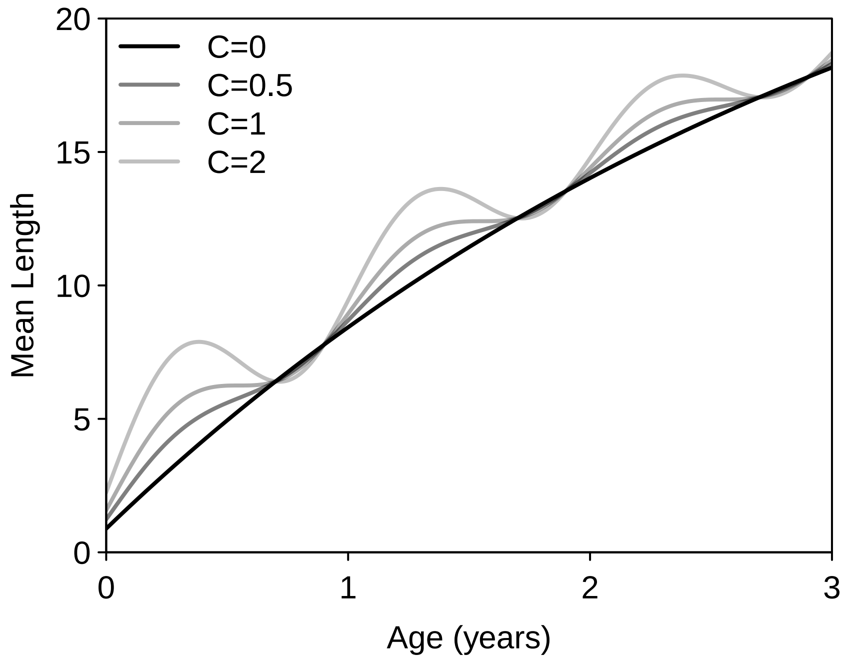

Figure 1: Example VBGF using Equation 3 with L_∞=30, K=0.3, t_0=-0.1, t_s=0.05 (or WP=0.55), and four different values of C.

Values of C>1 (or <0) in Equation 3 allow seasonal decreases in mean length-at-age (Figure 1). A decrease in mean length is unlikely for organisms whose skeletons largely preclude shrinkage (Pauly et al. 1992), although a seasonal decrease in mean length-at-age is possible if size-dependent overwinter mortality occurs (Garcia-Berthou et al. 2012). Pauly et al. (1992) modified Equation 3 to include a true seasonal no-growth period where mean length was not allowed to decrease and that included a smooth transition of the modeled mean length-at-age into and out of the no-growth period. Specifically, their modification is

$$\begin{aligned} q =& K^{'}(t^{'} - t_0) \\ &+ \frac{K^{'}(1 - NGT)}{2\pi} sin\left(\frac{2\pi}{1 - NGT}(t^{'} - t_s)\right) - \frac{K^{'}(1 - NGT)}{2\pi} sin\left(\frac{2\pi}{1 - NGT}(t_0 - t_s)\right) \end{aligned} \tag{4}$$

where NGT is the "no-growth time" or the length of the no growth period (as a fraction of a year) and $t^{'}$ is found by "subtracting from the real age (t) the total no-growth time occurring up to age t" (Pauly et al. 1992). Furthermore, Pauly et al. (1992) noted that the units of K changed from $year^{-1}$ in Equation 3 to $(1 - NGT)^{-1}$ in Equation 4. To eliminate confusion, they suggested using $K^{'}$ in Equation 4, as we do here.

Pauly et al. (1992) derived Equation 4 by assuming C=1 (i.e., that the rate of growth is 0 at the WP) and replacing 2π with $\frac{2\pi}{1-NGT}$ (i.e., restricting the oscillation to the period of growth and noting that $K^{'}$ only operates during this shorter period). Their modification may be described geometrically (though not algorithmically) in two steps. First, the seasonal growth function in Equation 3 with C=1 is fit to the observed lengths and ages that have had the cumulative NGT subtracted (i.e., using $t^{'}$). The growth trajectory is then separated at each WP and horizontal segments that are NGT units long are inserted at these points. This forms a growth trajectory that smoothly transitions into and out of the no-growth periods (Figure 2).

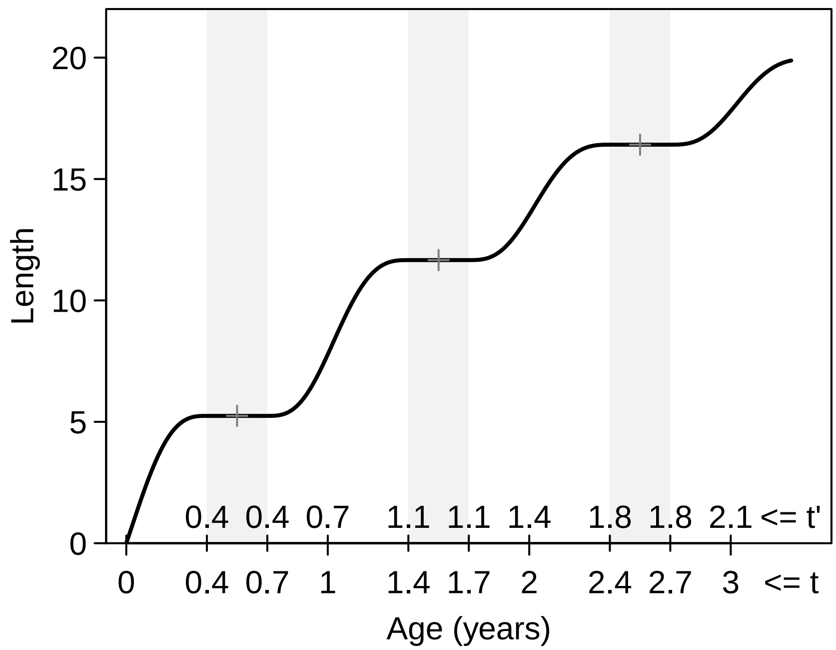

Figure 2: Example VBGF using Equation 4 or Equation 5 with L_∞=30, $K^{'}$=0.4286, t_0=0, NGT=0.3, and t_s=0.05 or WP=0.55. The no-growth periods are marked with gray bars and each WP is marked with a gray plus symbol. The ages adjusted for the NGT (i.e., $t^{'}$) are shown above the x-axis.

Pauly et al. (1992) provided a "diskette" that contained a computer program to estimate the parameters of Equation 4. The diskette is difficult (at best) to obtain and the source code is no longer available (D. Pauly, pers. comm.). Pauly et al. (1992) did describe the operations performed by their program, but there is no description of how $t^{'}$ was operationalized. This is an important step in using Equation 4 because $t^{'}$ is a function of t, but it is also a function of NGT and t_s, which are parameters to be estimated during the model-fitting process. In other words, the values for $t^{'}$ change with each iteration of the non-linear model-fitting process.

Therefore, the objectives of this note are to (i) describe a slight modification of Equation 4 that eases the calculation of $t^{'}$ while providing a more meaningful parameter; (ii) describe a function for calculating $t^{'}$ that may be used in the model-fitting process; (iii) provide an (open-source) algorithm for the modified function that can be used in model-fitting; and (iv) demonstrate the use of the modified function for fitting length-at-age data.

The Modified Seasonal Cessation Growth Function

In Equation 3, $WP = t_s + \frac{1}{2}$ because the sine function has a period of one year. The growth period is compressed in Equation 4 to be $1 - NGT$. Thus, the start of the no-growth period (SNG) is $t_s + \frac{1-NGT}{2}$. The center of the no-growth period is then $SNG + \frac{NGT}{2}$ or $t_s + \frac{1}{2}$. Thus, $WP = t_s + \frac{1}{2}$ is the center of the no-growth period for Equation 4.

By simple substitution, Equation 4 may be modified to include WP rather than t_s.

$$
\begin{aligned}
q =& K^{'}(t^{'} - t_0) \\
&+ \frac{K^{'}(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}\left(t^{'} - WP - \frac{1}{2}\right)\right) \\
&- \frac{K^{'}(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}\left(t_0 - WP - \frac{1}{2}\right)\right)
\end{aligned} \tag{5}
$$

As noted by Pauly et al. (1992) the calculation of $t^{'}$ depends on the observed age (t) and the cumulative no-growth time prior to t. In practice, the calculation of $t^{'}$ also depends on the position of the no-growth period within a year. Here, the position of the no-growth period is defined by SNG and NGT. However, because the SNG has a one-to-one relation with WP and t_s, the no-growth period can also be defined relative to these parameters.

The following algorithm is used to convert from observed ages (t) to ages adjusted for cumulative NGT prior to age t ($t^{'}$).

1. Shift the age (t) by subtracting the start of the no-growth period (SNG) from t, such that a whole number age represents the start of a no-growth period. For example, if SNG=0.4, then t=2.4 will become 2.0 and t=2.9 will become 2.5.
2. Subtract the whole number age from the shifted age such that the remaining decimal represents the fraction of a shifted year. For example, a 0 will result if the shifted age is 2.0 and a 0.5 will result if the shifted age is 2.5.
3. Substract the NGT from the value from the previous step.
4. If the value from the previous step is negative, then the age is within the no-growth period and the negative value should be replaced with a zero. Otherwise, the positive value represents the fraction of the growth period completed.
5. Add the value from the previous step to the total growth time completed (i.e., the product of the number of growth periods completed and the length of the growth period ($1 - NGT$)).
6. Compute t' by adding back the SNG that was subtracted in Step 1.

Further examples of $t^{'}$ values relative to t values are shown in Figure 2. This algorithm for computing $t^{'}$ is implemented in an R (R Development Core Team 2016) function as shown in Appendix 1. With this, Equation 6 is easly implemented as an R function as shown in Appendix 2.

Fitting the Modified Model

Simple simulated data were initially used to demonstrate the fitting of Equation 6. The data were simulated by randomly selecting 200 real numbers from a uniform distribution between 0 and 5 to serve as observed ages, plugging these ages into Equation 6 to compute a mean length for each age, and then adding a random deviate from a normal distribution with a mean of 0 and a standard deviation of σ to each mean length to simulate observed individual lengths. The `nls()` function from R was then used to estimate parameter values for Equation 6 from the simulated data. The "port" algorithm in `nls()` was used as L_∞ and $K^{'}$ were constrained to be positive and WP and NGT were constrained to be between 0 and 1. One would expect the parameter estimates to be very close to the values used to create the simulated data, as Equation 6 was used to both create and fit the data.

One example of a model fit to data that were simulated to have a "long" NGT, "late" WP, and low individual variability is shown in Figure 3. In this example, the parameter estimates are quite close to the parameter values used to simulate the data (the set parameter values are within the confidence intervals for each parameter).

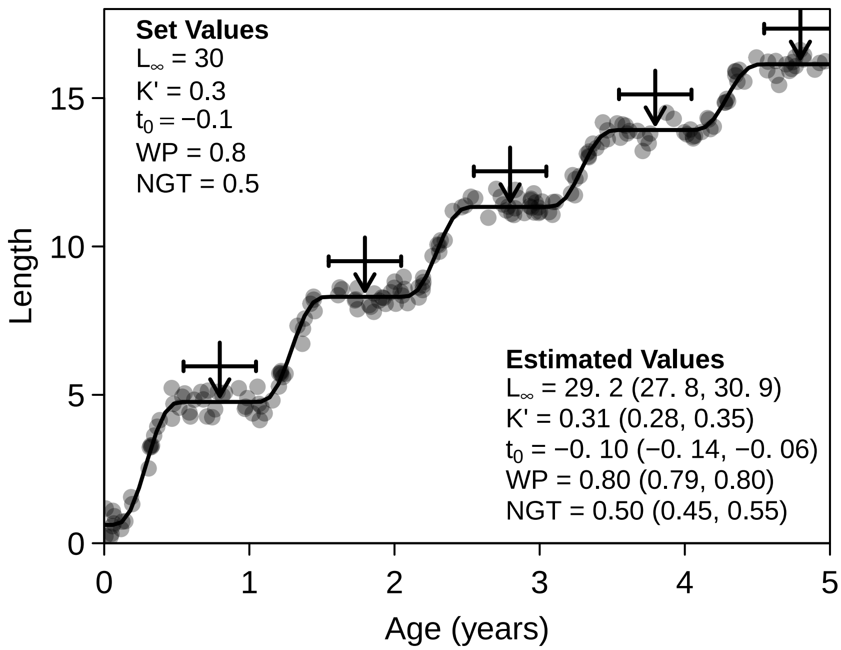

Figure 3: Example VBGF using Equation 5 with parameters shown in the upper-left corner and σ=0.3. Parameter estimates (and 95% confidence intervals) from non-linear regression are shown the lower-right corner. Each WP is shown by the arrow and each NGT is shown by the horizontal interval bar centered on the WP arrow.

Equation 6 was fit to simulated data sets that consisted of all combinations of "early" ($WP = 0.2$) and "late" ($WP = 0.8$) winter points, "short" ($NGT = 0.2$) and "long" ($NGT = 0.5$) no-growth periods, and "low" ($\sigma = 0.3$) and "high" ($\sigma = 0.5$) individual variabilities. These limited simulations suggest that all parameters are consistently well estimated, with the possible exception of t_0.

```
##      WPset NGTset sigmaset WPest WPlci WPuci NGTest NGTlci NGTuci Linfest
## [1,]   0.8    0.5      0.3  0.80  0.79  0.80   0.50   0.45   0.55    29.2
## [2,]   0.8    0.5      0.5  0.80  0.78  0.82   0.46   0.34   0.56    29.4
## [3,]   0.8    0.2      0.3  0.80  0.79  0.81   0.21   0.15   0.26    30.4
## [4,]   0.8    0.2      0.5  0.78  0.76  0.80   0.16   0.07   0.25    28.3
## [5,]   0.2    0.5      0.3  0.19  0.18  0.20   0.52   0.47   0.57    30.4
## [6,]   0.2    0.5      0.5  0.19  0.18  0.21   0.57   0.48   0.65    31.2
## [7,]   0.2    0.2      0.3  0.21  0.20  0.22   0.16   0.11   0.20    30.0
## [8,]   0.2    0.2      0.5  0.21  0.19  0.23   0.15   0.06   0.23    29.4
##      Linflci Linfuci Kest Klci Kuci t0est t0lci t0uci
## [1,]    27.8    30.9 0.31 0.28 0.35 -0.10 -0.14 -0.06
## [2,]    26.9    32.8 0.29 0.23 0.36 -0.13 -0.22 -0.05
## [3,]    29.6    31.2 0.30 0.28 0.32 -0.15 -0.23  0.03
## [4,]    27.4    29.4 0.32 0.29 0.36  0.06  0.02  0.09
## [5,]    28.8    32.2 0.31 0.27 0.35 -0.13 -0.17    NA
## [6,]    28.2    35.3 0.33 0.26 0.43 -0.15 -0.20    NA
## [7,]    29.4    30.7 0.29 0.27 0.31 -0.07 -0.09 -0.05
## [8,]    28.4    30.6 0.29 0.26 0.33 -0.07 -0.11 -0.03
```

Real Data

Stewart et al. (2013) examined the growth of 215 Bonito (*Sarda australis*) sampled from commercial landings. Detailed methods are described in Stewart et al. (2013), but note here that fork lengths (mm) were measured for each fish and ages were the decimal age calculated as the number of opaque zones observed on otolith thin sections plus the proportion of the year after the designated birthdate. Stewart et al. (2013) fit Equation 3 to these data but constrained C to be less than 1. Their model fit resulted in the boundary condition of $C = 1$, which suggested that Bonito ceased to grow at *at least* one point. As C is at least equal to 1, this result also suggests that Equation 6 should be fit to these data to determine the length of the no-growth period (Pauly et al. 1992). Thus, Equation 6 is fit to these data here as an example of fitting Equation 6 to real data.

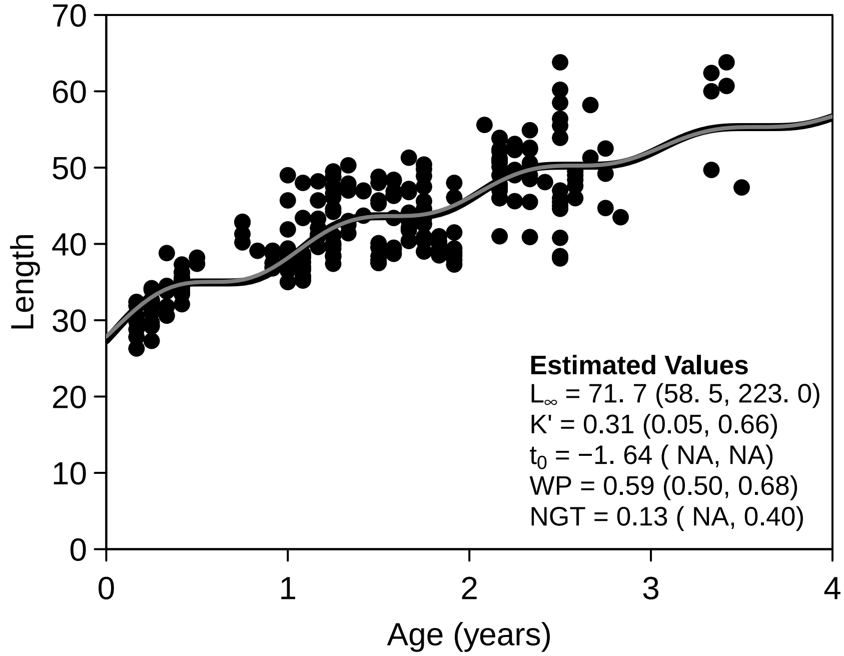

Figure 4: Fork length at age for Australian Bonito with the best-fit of Equation 5 (black line) and Equation 3 (gray line) superimposed. The parameter estimates (and 95% confidence intervals) from non-linear regression for Equation 5 are shown the lower-right corner.

Discussion

- General – fits perfectly simulated data well.
- Assumptions – WP same time each year and age, NGT same length each year and age
- Model-Fitting – bounding parameters, more difficult to fit five parameters
- Practical Difference – not large unless C>>1 and NGT>>0

Appendices

Appendix 1

```
################################################################################
## internal function to compute t-prime
```

```
################################################################################
iCalc_tpr <- function(t,WP,NGT) {
  ## Step 1
  SNG <- WP-NGT/2
  tmp.t <- t-SNG
  ## Step 2 (in parentheses) and Step 3
  tmp.t2 <- (tmp.t-floor(tmp.t)) - NGT
  ## Step 4
  tmp.t2[tmp.t2<0] <- 0
  ## Step 5 (in parentheses) and Step 6 (also returns value)
  (floor(tmp.t)*(1-NGT)+tmp.t2) + SNG
}
```

Appendix 2

```
################################################################################
## Main Function
##   Linf, t0 as usual
##   Kpr = K-prime as defined in Pauly et al. (units are diff than usual K)
##   WP = "Winter Period" (middle point of no-growth period) = ts+0.5
##   NGT = "No Growth Time" = "fraction of a year where no growth occurs"
##   tpr = "t-prime" = actual age (t) minus cumulative NGT prior to t
################################################################################

VBSCGF <- function(t,Linf,Kpr=NULL,t0=NULL,WP=NULL,NGT=NULL) {
  if (length(Linf)==5) { Kpr <- Linf[[2]]; t0 <- Linf[[3]]
  WP <- Linf[[4]]; NGT <- Linf[[5]]
  Linf <- Linf[[1]] }
  tpr <- iCalc_tpr(t,WP,NGT)
  q <- Kpr*(tpr-t0) +
    (Kpr*(1-NGT)/(2*pi))*sin((2*pi)/(1-NGT)*(tpr-WP+1/2)) -
    (Kpr*(1-NGT)/(2*pi))*sin((2*pi)/(1-NGT)*(t0-WP+1/2))
  Linf*(1-exp(-q))
}
```

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